

THE EVOLUTION OF ANTARCTIC FISHES: QUESTIONS FOR CONSIDERATION AND AVENUES FOR RESEARCH

by

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ABSTRACT. - This paper is derived from the keynote address given at a workshop entitled "Technical and Theoretical Approaches to Antarctic Fish Evolution". The workshop was held in Santa Margherita Ligure, Italy from October 8-10, 1994 and was sponsored by a European Science Foundation Network Proposal entitled "Fishes of the Antarctic Ocean". The paper introduces the theme of the workshop and focuses on these aspects of notothenioid evolution: 1) the Cenozoic fossil record for fishes in Antarctica with a hypothesis for the emergence of notothenioids; 2) the composition of the modern fauna; 3) a comparison of the diversifications experienced by notothenioids and other teleosts and 4) the nature of adaptations to the Antarctic marine environment. The following are recommended objectives for future multidisciplinary research on notothenioids: 1) production of cladograms resolved to the level of genus and species; 2) comparison of cladograms produced from different data sets and combination of different types of characters into a single large data set; 3) expansion of the taxonomic base and suites of characters available for cladistic analysis; 4) evaluation of the roles of phylogeny and environmental adaptation in the diversification of notothenioids; 5) employment of divergence times inferred from molecular data to evaluate palaeoenvironmental changes as vicariant events influencing notothenioid diversification; 6) maintenance of research focused on both microevolutionary and macroevolutionary levels and 7) incorporation of marine biodiversity issues into notothenioid research.

RÉSUMÉ. - Cet article est tiré d'une conférence qui a été donnée au cours d'un "workshop" intitulé "Technical and Theoretical Approaches to Antarctic Fish Evolution". Ce workshop s'est déroulé à Santa Margherita (Ligure, Italie) du 8 au 10 octobre 1994 et était soutenu financièrement par un "European Science Foundation Network Proposal" intitulé "Fishes of the Antarctic Ocean". Cet article introduit le thème du "Workshop" et s'intéresse plus particulièrement aux aspects de l'évolution des Notothenioidei: 1) les fossiles Cénozoïque des poissons en Antarctique avec une hypothèse sur l'émergence des Notothenioidei; 2) la composition de la faune moderne; 3) une comparaison des diversifications subies par les Notothenioidei et d'autres Téléostéens; 4) la nature des adaptations à l'environnement marin antarctique. Les objectifs suivants sont recommandés pour de futures recherches multidisciplinaires sur les Notothenioidei: 1) la construction de cladogrammes résolus au niveau du genre et de l'espèce; 2) la comparaison de cladogrammes construits à partir de différentes bases de données et la combinaison de différents types de caractères en une seule grande banque de données; 3) l'extension de la base taxinomique et des suites de caractères disponibles pour l'analyse cladistique; 4) l'évaluation des rôles de la phylogénèse et de l'adaptation à l'environnement dans la diversification des Notothenioidei; 5) l'utilisation de temps de divergences obtenus à partir de données moléculaires pour évaluer les changements du paléoenvironnement comme des événements vicariants influençant la diversification des Notothenioidei; 6) la poursuite de recherches centrées à la fois sur les niveaux de la micro et de la macroévolution et 7) l'incorporation des données sur la biodiversité marine dans la recherche sur les Notothenioidei.

Key-words. - Notothenioids, Antarctic Ocean, Evolution.

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Component groups of the "Fishes of the Antarctic Ocean" network have a shared curiosity about the evolution of the Antarctic fish fauna and a desire to contribute to the solution of broad evolutionary problems. This fauna is attracting increasing notice from the biological community at large. For example, in the first chapter of his book *The Diversity of Life*, Edward O. Wilson (1992, p. 14) advocates increased attention to the biological wealth of our planet and cites Antarctic fishes as an example of one extreme in the spectrum of animal diversification and adaptation. Although the initial descriptions of Antarctic fishes began appearing in the mid 1800's, we have just begun to closely examine the nature of their diversification within the Antarctic marine ecosystem. Ongoing studies of molecular, organ system and organismal diversification will elucidate the biological modifications necessary for life in Antarctic waters. Research projects included in the "Fishes of the Antarctic Ocean" Network touch on a number of major themes in modern evolutionary biology including: 1) the adaptive fit between organisms and a unique environment, more specifically the influence of this environment on levels of biological organization ranging from molecules to organisms to communities; 2) the relationship between phyletic divergence and palaeoenvironmental events; 3) the nature of biological diversity in polar waters compared with other habitats; 4) mechanisms of speciation and 5) the analysis of phylogenetic relationships using cladistic methodology and new suites of characters.

In keeping with this evolutionary theme, this paper will emphasize these topics with an eye toward what is not known: 1) the Cenozoic fossil record for fishes in Antarctica with a hypothesis for the emergence of notothenioids; 2) the composition of the modern fauna; 3) a comparison of the diversifications experienced by notothenioids and other teleosts and 4) the nature of adaptations to the Antarctic marine environment. In concluding I suggest some avenues for research that might enhance our understanding of notothenioid evolution, areas that might benefit from a multidisciplinary approach.

Before beginning, a few definitions are in order. In terms of the fishes, I deal exclusively with notothenioids. In referring to members of the family Nototheniidae, I employ the nomenclature of DeWitt *et al.* (1990). My use of the term diversity may be taken as synonymous with species richness. Diversification means phyletic divergence which, in some notothenioid subgroups, has been accompanied by considerable ecological divergence. I follow conventional abbreviations in geology by using mya to denote millions of years ago in general and Ma to indicate an absolute age in millions of years.

Historical changes in Antarctic fish diversity

The fossil record

When available, a fossil record provides an approximate time of appearance for the group under consideration. It also offers a long term perspective on faunal change. Many of the modern percomorph families, for example, probably evolved rapidly during the late Cretaceous (98-65 Ma), with some modern genera emerging during the Eocene (55-38 Ma) (Carroll, 1988). A purported notothenioid fossil has recently come to light as a result of the reanalysis of a previously described non-notothenioid. A partial skull from the La Meseta Formation on Seymour Island (Antarctic Peninsula) was described by Eastman and Grande (1991) as a late Eocene (38 Ma) gadiform. Balushkin (1994) has subsequently identified this skull as that of a basal nototheniid related to the extant *Eleginops* of South America. If Balushkin's identification is correct, this fossil provides an approximate time of appearance for notothenioids in an Antarctic locality of about 60°S palaeolatitude.

Although the fossil record for notothenioids is sparse, we have a reasonably extensive record for non-notothenioid fishes living in the region of Seymour Island during the late Eocene (Eastman, 1993). This affords some insight into environmental conditions at the time and presents an interesting evolutionary issue.

There is striking disparity between the diverse, cosmopolitan late Eocene fauna from Seymour Island and the endemic modern fauna dominated by notothenioids. In the light of new discoveries, this disparity has continued to widen. To the Seymour Island ichthyofauna, Douglas Long has recently added a cutlassfish (1991), a wrasse (1992a) and a number of new sharks bringing the total number of shark taxa to 17 (1992b). As part of the Weddell Zoogeographic Province, this area had extensive shallow shelf habitat washed by warm seas. Under these conditions we would expect a diverse ichthyofauna. It is remarkable, however, that there has been little persistence of taxa into the modern fauna. This is not the case elsewhere in the Southern Hemisphere. There is, for example, good taxonomic correspondence between the Tertiary (Oligocene/Miocene) and Recent ichthyofaunas of Australia - many of the same chondrichthyan and teleostean genera are present in both faunas (Long, 1982). In the section below on the modern fauna, I will consider the reasons for the discrepancy between the fossil and modern faunas of Antarctica.

Another intriguing recent development centers on the discovery of fossils of taxonomically diverse cetaceans, including dolphins, in marine Pliocene (4.2-3.5 Ma) deposits in the Vestfold Hills area of East Antarctica (Quilty, 1993, 1994). These deposits, including unidentified fish (Quilty, 1994), were assumed to have been laid down under relatively warm water conditions. This is an especially important site because it narrows the 38 Ma gap in the fossil record for Antarctic fish and suggests that Pliocene nearshore ecosystem may have been more diverse, and less like the modern ecosystem, than previously expected.

A hypothesis for the diversification of notothenioids

The breakup of Gondwana and the subsequent development of the pattern of ocean currents around Antarctica certainly influenced the composition of the Antarctic fish fauna. Antarctica was separated from other land masses by seafloor spreading and deep water in the Drake Passage at about the Oligocene/Miocene boundary 25 Ma. These tectonic and oceanographic events isolated Antarctica and initiated climatic changes that probably eliminated some habitats available to the Seymour Island fish fauna. The diversity of the fauna was reduced and the taxonomic composition was changed over geologic time. Although water temperatures began to fall during the Eocene, I am in agreement with Andrew Clarke (1993, for summary) that low water temperature by itself was not the overriding factor in causing this faunal change. Instead inshore habitat and faunal destruction by ice, changing trophic conditions and the grounding of ice shelves as far as the shelf break in some areas, may have caused the local extinction of some of the early Tertiary non-notothenioid fauna.

Notothenioids were most likely associated with the shelf of the Weddell Province since the late Cretaceous or early Tertiary. They probably diversified through mechanisms of both vicariance and dispersal. Diversification was facilitated by the thermal isolation of Antarctica, by the increasing productivity of the Southern Ocean beginning about 22 Ma (Kennett, 1982) and by the absence of competition from non-notothenioids. The midwaters of the developing Southern Ocean were, in an evolutionary sense, underutilized by fishes, and this ecological space was filled by a diversifying notothenioid

fauna tolerant of deeper and colder habitats. Notothenioids underwent a depth-related diversification directed away from the ancestral benthic habitat toward pelagic or partially pelagic zooplanktivory and piscivory. They have come to occupy niches normally held by taxonomically diverse fishes in other shelf areas of the world (Eastman, 1993). Divergence times calculated from molecular data, suggest that the radiation of some notothenioid subgroups took place more recently than we had previously suspected (Bargelloni *et al.*, 1994, 1995; Ritchie *et al.*, 1996).

Once the modern fauna was established, low water temperatures, extreme geographic isolation and lack of south flowing surface currents limited immigration of many Southern Hemisphere epipelagic and mesopelagic groups into waters south of the Antarctic Polar Front.

The modern Antarctic fish fauna

Size

Unlike faunas of other large marine ecosystems, the Antarctic fish fauna is small in size and limited in taxonomic diversity. With worldwide fish diversity estimated at 24,618 species in 482 families (Nelson, 1994), the Southern Ocean contains only 274 species in 49 families (Gon and Heemstra, 1990). Thus the Southern Ocean, representing 10% of the world's ocean, accommodates only about 1% of the world's fish fauna. The fauna is highly endemic, with 88% of the species confined to the Antarctic Region (Andriashev, 1987). As judged by the number of species and families, marine fish diversity is considerably greater in adjacent cold temperate regions of the Southern Hemisphere. For example, Tasmanian waters support 459 species in over 150 families (Last *et al.*, 1983). The waters within 200 miles of New Zealand contain 1008 species in 208 families (Paulin *et al.*, 1989). Rather than dwelling on the restricted taxonomic diversity, perhaps we should view the Southern Ocean and its ichthyofauna from a different perspective. Given the unavailability of some major habitats, it is surprising that Antarctic waters support so many species. Antarctic coastal waters are without estuaries, reefs, intertidal zones and shallow continental shelves - prime areas for fish diversity and biomass elsewhere in the world.

Why is the modern Antarctic fauna so different from those of other southern continents when all shared a common late Cretaceous/early Tertiary fauna? The answer probably lies in the regional historical processes mentioned previously, especially tectonic, oceanographic and climatic events. These processes are important in establishing patterns of diversity in polar marine organisms (Brey *et al.*, 1994). With the breakup of Gondwana, each southern landmass and its shelf fauna became independent and influenced by different historical processes. As the Tertiary progressed, Antarctic shelf waters became increasingly isolated and subject to current patterns, glacial scour, changing temperatures, marked seasonality and altered trophic conditions. These events, coupled with an element of chance, produced the distinctive modern fish fauna inhabiting the Southern Ocean. We might also note the absence of similarity between the two polar fish faunas. The Arctic fauna is younger and lacks a monophyletic radiation, equivalent to notothenioids, into a variety of water column habitats. Instead, the Arctic fauna consists of phylogenetically diverse fishes including cods, eelpouts, sculpins, snailfishes, flatfishes, herrings, salmon and smelts (Andriashev, 1954). Unfortunately we lack an up to date faunal and taxonomic treatise for the Arctic fishes, and this tends to inhibit research in comparative biology.

Dominance by notothenioids

The fish fauna of the Southern Ocean surrounding Antarctica holds the attention of evolutionary biologists for a number of reasons. With six families and 122 species, the perciform suborder Notothenioidei commands the overwhelming share of species diversity. In the entire Southern Ocean, about 35% of species are notothenioids; in subzero shelf and slope waters 55% are notothenioids (Gon and Heemstra, 1990). Here they occupy most benthic and water column habitats, accounting for 90-95% of the biomass (DeWitt, 1971; Ekau, 1990). In the eastern and southern Weddell Sea, 94% of the specimens captured are members of the family Nototheniidae (Hubold, 1991). This is an exceptional degree of habitat saturation by a single taxonomic group. Nineteen new species of notothenioids have been described between 1980 and 1993; additional new species will certainly come to light. As judged by the recent description of a meter long pelagic predator (*Gvozdarus svetovidovi* Balushkin, 1989), it is also safe to say that we do not have a full appreciation of either the taxonomic or ecological diversity in the suborder. Interestingly, with 14 species the largely non-Antarctic nototheniid genus *Patagonotothen* is now the most speciose in the suborder.

In addition to phyletic diversification and unlike most other vertebrate and fish groups (Brooks and McLennan, 1991, 1992; Mayden, 1992), notothenioids have also experienced substantial ecological diversification - there are a number of life history or ecological types. In a habitat underutilized by other fish groups, notothenioids underwent a depth-related diversification centered on the evolutionary alteration of buoyancy and the morphology associated with swimming and feeding in the water column. They occupy niches filled by taxonomically unrelated fishes in temperate and tropical oceans. Although lacking swim bladders, some notothenioids diversified away from the ancestral benthic habitat toward pelagic or partially pelagic zooplanktivory and piscivory. Within the family Nototheniidae, for example, about 50% of the Antarctic species are pelagic, semipelagic, cryopelagic or epibenthic rather than benthic, the presumed ancestral type (Eastman, 1993). Some notothenioids are close to neutral buoyancy and permanent or temporary (for purposes of feeding) members of the water column community. It is possible that some notothenioid clades coevolved with water column resources like krill.

Often referred to as pelagization, this ecomorphological trend toward life in the water column in nototheniids has been admirably documented by Klingenberg and Ekau (unpubl. data) for 10 species in the nototheniid subfamilies Trematominae and Pleuragramminae. Their morphometric study demonstrated the phyletic component of pelagization; pelagic life styles have arisen in the clade of epibenthic trematomids (*Trematomus loennbergii*, *T. lepidorhinus* and *T. eulepidotus*) and in the pleuragrammins. Their study also suggests that phylogenetically related species are not necessarily morphologically and ecologically similar.

Notothenioids compared with other teleostean diversifications

Compared with other shelf habitats, the fish fauna of the Antarctic shelf is taxonomically unbalanced, with notothenioids holding the overwhelming share of total fish species diversity - a striking example of the nature of Antarctic marine biodiversity. As evolutionary biologists we are interested in how this has come to be and whether there are similar situations elsewhere. While there are other marine perciform groups that greatly exceed the species diversity of notothenioids, there is no group that exhibits similar ecological diversification and dominance of a continental shelf habitat. In some respects notothenioids resemble the species flocks from large lakes: cichlids in the Great Lakes of

East Africa's Rift Valley, cottoids in Lake Baikal in Siberia and cyprinids in Lake Lanao in the Philippines (Greenwood, 1984; Ribbink, 1984; Echelle and Kornfield, 1984). The cottoids are most similar to notothenioids in that they are a swim bladderless group of marine origin. The species in Lake Baikal have undergone a "depth related ecological divergence" (Smith and Todd, 1984), similar to but not as extensive as that of the notothenioids. About half the fish species in Lake Baikal are cottoids including benthic, epibenthic and pelagic species, some of the latter are close to neutral buoyancy (Kozhov, 1963). Interestingly, only four of 29 (14%) species are epibenthic or pelagic (Sideleva *et al.*, 1993), much lower than the 50% figure for Antarctic notothenioids.

With the exception of the Baikal cottoids, none of the lacustrine diversifications are of comparable antiquity to the notothenioids, and some are very young. On the basis of sequences in mitochondrial DNA, the 200 species of haplochromine cichlids in Lake Victoria are thought to be monophyletic and to have diverged in the past one million years (Meyer *et al.*, 1990).

Notothenioids differ from lacustrine species flocks in the following respects: monophyly has not been unequivocally demonstrated, they are marine and they are older than most other species flocks. Although diversity (about 122 species) is modest compared with the large size of the ecosystem, their ecological dominance in Antarctic shelf waters is unparalleled when compared with other marine groups in other shelf habitats. The diversification of some notothenioid clades may have been linked to increasing productivity in the Southern Ocean, but their radiation involves more than just trophic specialization and, for the most part, they do not exhibit fine division of trophic resources. While they may lack evolutionary novelties at the morphological level of organization, there has been substantial ecological (life history) diversification similar in magnitude to that displayed by taxonomically disparate fishes elsewhere in the world. Phrased in another way, the morphological diversification of notothenioids is proportionally less than we would expect given our knowledge of their ecological diversification. This may be unique in the marine realm.

Notothenioids may not be an example of an adaptive radiation using the narrow criteria applied to lacustrine species flocks. However they do qualify as an adaptive radiation using a less restrictive definition (Brooks and McLennan, 1991, p. 182): "hypotheses of adaptation are strongest when we can compare convergent acquisitions of traits under similar environmental conditions". I think that the most obvious examples of convergent (homoplastic) features in notothenioids are those associated with pelagic life. I suggest that the "adaptation" in notothenioids has been their evolutionary accommodation to underutilized ecological space in the water column, and that their adaptive radiation has been keyed to the use of this space.

What features of notothenioids are adaptive to the Antarctic marine environment?

We could define an adaptation as an apomorphic (derived) character state associated with the environmental conditions under which a species is currently living (Brooks and McLennan, 1991, p. 145). Ideally some selective advantage could be experimentally demonstrated (i.e., possession of the trait would increase the fitness of the organism). We are just beginning to take a critical approach in evaluating adaptations, but let us see how this definition applies to some features of the morphology of notothenioids. Hypotheses of adaptation to polar conditions would be strengthened by the independent acquisition of

traits in phylogenetically unrelated groups like notothenioids and Arctic fishes. With the exception of antifreezes, however, the Arctic fauna has been little studied in this respect.

At first glance there is nothing striking about the outward appearance of notothenioids. Adaptation to the cold and highly seasonal Antarctic marine environment has entailed little alteration of the basic perciform body. As far as our knowledge extends, this diversification has been accomplished without the evolution of novel morphology. We have not discovered anything comparable to the key innovations in pharyngeal morphology (development of joints and shift in muscle insertions) that allowed cichlid pharyngeal jaws to masticate food thereby freeing the oral jaws for extremely diverse collecting functions (Liem, 1973). This may have played a role in the radiation of the clade.

The organ systems of notothenioids do not display a suite of gross anatomical or histological features that are obviously related to physical features of the Southern Ocean. We know, for example, that eyes and brains are not morphologically specialized for the unusual light cycle nor skin and gills for the presence of ice. At the ultrastructural level of organization we do encounter some differences between notothenioids and temperate teleosts, but these are differences in degree rather than in kind. Examples include the proliferation of mitochondria and the expansion of oxidative enzyme systems in red pectoral muscle, and the prominence of perisinusoidal cells in the liver of *Dissostichus mawsoni*. So most cellular, tissue and organ level adaptations can also be found in non-notothenioid lineages. The fact that the basic perciform morphology serves as well in a polar habitat as it does in the tropics may partially explain the success of this largest order of vertebrates with over 9,200 species.

At the organismal level, however, many of the evolutionary alterations for neutral buoyancy and life in water column are morphological, and these characters are different than the plesiomorphic notothenioid condition as exemplified by bovichtids or the basal nototheniid *Eleginops maclovinus*. Examples include morphometric measurements, partially cartilaginous skeleton, persistent notochord and unusual lipid storage systems (large sacs). If we consider pedomorphosis to fall within the realm of morphology, this evolutionary change in the ontogenetic timing of certain aspects of organogenesis has been important in the diversification of radically different ecological types - the neutrally buoyant *Pleuragramma antarcticum* is the best example (Balushkin, 1984). In this species the notochord of larvae is retained in adults (Totton, 1914), resulting in a significant reduction in density (DeVries and Eastman, 1978). Although always vital for zoogeographical, ecological and fishery management studies (North, 1991; Kock, 1992; Loeb *et al.*, 1993), knowledge of notothenioid larval biology can also provide insight into evolutionary processes. For example, Klingenberg and Ekau (unpubl. data) infer from their analysis of adults that the morphometric differences reflecting various degrees of pelagization in trematomids are established in larval life.

There may be undiscovered innovations at the biochemical and physiological levels of biological organization. As far as our knowledge extends, however, it seems that refinements of physiological and biochemical processes, rather than innovations, are characteristics of notothenioid organ systems. Especially prominent and well studied are mechanisms that prevent freezing (DeVries, 1988; Cheng and DeVries, 1991) and that allow normal cellular, tissue and organ function at subzero temperatures (Macdonald *et al.*, 1987; Wells, 1987; di Prisco and D'Avino, 1989; di Prisco *et al.*, 1990, 1991; Johnston, 1989; Johnston *et al.*, 1991; Crockett and Sidell, 1990; Londraville and Sidell, 1990; Lund and Sidell, 1992; Kunzmann, 1991; Montgomery and Wells, 1993). If tissues are protected by freezing resistance adaptations and if the physiology of excitable

tissues has been adjusted to deal with the slowing effect of low temperature on molecular events in muscles and nerves, perciform physiology performs admirably under Antarctic conditions. It is also possible that some physiological "adaptations" in notothenioids may not confer any selective advantage in the Antarctic environment. The loss of the choroid rete, kidney glomeruli and haemoglobin may be cited as examples of questionable adaptations to low temperature for which there are alternative explanations. Within the most derived notothenioid families, these losses may simply reflect a phyletic trend toward organ system streamlining for energetic efficiency under constant environmental conditions. With the exception of haemoglobin, these reductions have also occurred in other lineages of marine teleosts.

Avenues for future research

Multidisciplinary approaches hold the promise of enhancing our understanding of the evolutionary biology of notothenioid fishes. I see the following areas as worthy of future research. Each is cast as an objective followed by additional comments.

Production of well supported cladograms resolved to the level of genus and species especially for the family Nototheniidae

Cladograms are absolutely necessary for answering the evolutionary questions we are pursuing. Powerful computer programs like *PAUP* (Swofford, 1993) are available for this purpose. What use are cladograms to scientists not conducting research in systematic biology? If we are going to properly apportion the results of our studies (i.e., our ecological, morphological, physiological, biochemical data) between characters that are possibly synapomorphic for notothenioids (or certain notothenioid subgroups) and characters that are plesiomorphic, we must have an accurate cladogram as a template for analyzing our data. Or phrased in another way, we must know what persistent ancestral traits notothenioids brought into this natural experiment, and this cannot be done without an historical frame of reference.

Cladograms for notothenioids provide a means for exploring interesting evolutionary questions related to the uniqueness of the fauna. This approach projects our interests to biologists at large who will appreciate these questions and will therefore understand our interest in the fauna. We have, for example, begun to do this by mapping freezing resistance adaptations on a cladogram for notothenioids and then asking when and how many times these characters arose.

A model study of this sort is Barbara Block's (Block *et al.*, 1993) examination of the evolution of endothermy in scombroids. Since scombroid relationships based on morphological characters were ambiguous, Block produced a molecular phylogeny for 29 scombroid species based on sequences of part of the mitochondrial cytochrome b gene. Mapping the incidence of endothermy on the resulting independently derived cladogram suggests that the ability to warm the brain and eyes arose independently in three lineages. In each case this was associated with niche expansion into colder waters.

Evaluate the similarities and differences between cladograms derived from different data sets

Is there congruence between various data sets and between cladograms derived from, for example, morphological and molecular data sets? Agreement among cladograms generated from independent data sets lends additional support to hypothesized

relationships. Furthermore, different types of characters should be combined into a single large data set, and this should be subjected to cladistic analysis.

Since interrelationships among many perciform suborders are unknown (Johnson, 1993), an outgroup to notothenioids has not been established. Possible outgroups include zoarceoids (Anderson, 1990) and trachinoids (Hastings, 1993). Furthermore, the monophyly of notothenioids has not been unequivocally established through the use of osteological characters. A number of cladograms for notothenioids and for notothenioid subgroups have appeared in the last few years. For the suborder, we have cladograms based on: 1) largely osteology and recognizing eight (rather than the usual six) families (Balushkin, 1992); 2) osteology (drawn from Eakin, 1981 and Iwami, 1985) as well as a few soft tissue characters (Eastman, 1993); 3) osteology (Hastings, 1993) and 4) DNA sequences in 12S and 16S ribosomal RNA genes from mitochondrial DNA (Bargelloni *et al.*, 1994, 1995). For the family Nototheniidae, Klingenberg and Ekau (unpubl. data) produced a cladogram based on characters from the lateral line, skeleton, scales and larval pigment patterns. Finally, for the nototheniid subfamily Trematominae, we have a cladogram derived from DNA sequences in 12S and 16S ribosomal RNA genes from mitochondrial DNA (Ritchie *et al.*, 1996).

Figure 1 provides examples of cladograms generated from morphological (Eastman, 1993) and molecular data (Bargelloni *et al.*, 1994). The most noteworthy difference centers on the relationships among species of the family Nototheniidae. The molecular data suggest that, as currently recognized, the family is not monophyletic.

Broaden the taxonomic base (the species included) and the suites of characters available for cladistic analysis of notothenioids

More species and additional characters should yield more robust cladograms. There is considerable homoplasy in some of the osteological characters in current use. Other body systems have been little utilized as a source of characters. As mentioned above, phylogenies based on molecular data sets are beginning to appear (Bargelloni *et al.*, 1994, 1995; Ritchie *et al.*, 1996). We have a relatively large and growing karyological data set for notothenioids (Ozouf-Costaz, 1989; Morescalchi *et al.*, 1992a, 1992b; Prirodina, 1994), but it has not yet been subject to cladistic analysis.

We need to increase the knowledge base of morphological, physiological and biochemical characters for basal nototheniids so that characters can be correctly polarized for the phyletically derived groups living in the cold waters close to the continent. I think it would be worthwhile to focus on *Eleginops maclovinus* - the probable sister group to all other notothenioids. Based on osteological evidence, this species is the basal nototheniid (Balushkin, 1984; Voskoboynikova, 1993). Bovichtids probably diverged too early (57-45 mya) from the notothenioid stock to serve as the ideal sister group for the purpose of polarizing characters. These divergence times are inferred from molecular evidence (Bargelloni *et al.*, 1994, 1995).

We have little information about soft tissue anatomy, haemoglobin components and antifreeze, for example, in most non-Antarctic and sub-Antarctic nototheniids, harpagiferids and artedidraconids. Even if cladograms are ultimately derived from molecular data, we need to know more about the morphology, physiology and biochemistry of body systems in basal groups to evaluate the characters that we find in phyletically derived groups.

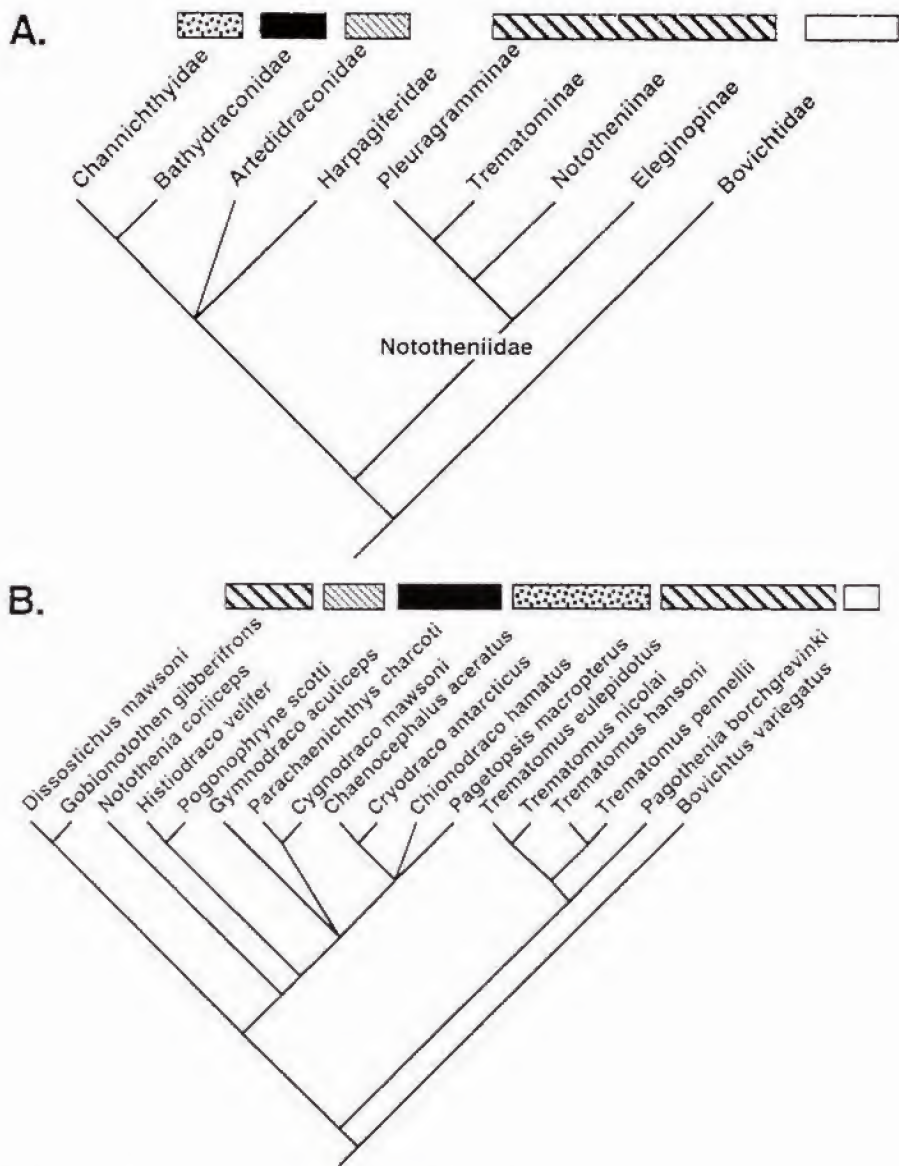


Fig. 1. - Cladograms depicting hypotheses of phylogenetic relationships for notothenioids. Cladograms were produced by the analysis of different data sets using maximum parsimony. **A.** Cladogram based on morphological characters modified from Eastman, 1993. Relationships among nototheniid subfamilies are not supported by a cladistic analysis. Shaded bars indicate limits of traditional notothenioid families. **B.** Cladogram based on DNA sequences in 12S and 16S ribosomal RNA genes from mitochondrial DNA (modified from Bargelloni *et al.*, 1994). This analysis suggests that, as traditionally conceived, the Nototheniidae is an unnatural group (paraphyletic).

Examples of soft tissue (brain) characters of possible use in the phylogenetic analysis of notothenioids include: expanded proximal olfactory nerves, size and shape of the corpus cerebelli and expanded ventricular margins in the diencephalon (Eastman and Lannoo, 1995).

Evaluate the roles played by phylogeny and environmental adaptation in the diversification of notothenioids

This question can be approached by analysis of ecological, morphological, physiological and biochemical data in a phyletic framework.

We have available a new research protocol in comparative biology, emphasizing an initial evaluation of data in a phyletic (historical) context rather than from a strictly adaptationist perspective (Brooks and McLennan, 1991, 1992; Mayden, 1992; Mayden and Wiley, 1992; Swofford and Maddison, 1992). Inheritance of a particular character from ancestors is the first order explanation or the evolutionary null hypothesis. Only characters that can be demonstrated as novel or diagnostic of a clade (autapomorphies) are considered for explanations that invoke environmental conditions unique to that clade (Brooks and McLennan, 1992, p. 89). Therefore to explore the evolution of characters, data are mapped on cladograms independently derived from other information. Based on the phylogenetic distribution of these features, it is possible to determine the plesiomorphic and apomorphic nature of characters, to see when they first appeared in a particular clade and whether they evolved more than once. An approach framed explicitly in terms of character change on a phylogeny provides a direct and powerful method of testing hypotheses in comparative biology (Swofford and Maddison, 1992). The mechanics of this procedure are simplified through use of computer programs such as *MacClade* (Maddison and Maddison, 1992).

Since Antarctic fishes live in an environment viewed by humans as extreme, there is a natural tendency to ascribe various aspects of their biology as adaptive to this habitat. Having cladograms allows us control for the phyletic (historical) component of a character before invoking environmental adaptation as a causative factor.

As an example of a phyletic effect (lineage specific variation), we could cite the large size and distinctive shape of the corpus cerebelli in the *coriiceps* group of *Notothenia* (*N. angustata*, *N. coriiceps*, *N. microlepidota*, *N. rossii* and *Paranotothenia magellanica*) (Eastman and Lannoo, 1995). Is this morphology an adaptation to a complex life cycle involving long distance dispersal of silvery pelagic juveniles and adult habitat shifts between benthic and pelagic (or semipelagic) life styles? Probably not, it is a plesiomorphic character for notothenioids when *Eleginops maclovinus* is used as a sister group; *Eleginops* also has a large cerebellum and a complex life cycle.

By serving as evolutionary markers, morphological and physiological characters (such as aglomerular kidneys and antifreeze glycopeptides) may help to resolve taxonomic and biogeographic controversies. This is especially true for little studied non-Antarctic and sub-Antarctic species. A case in point is the finding that two species of *Patagonotothen* from South America have aglomerular kidneys (Eastman and DeVries, unpubl.). This suggests a possible northward dispersal from Antarctica after acquisition of freezing resistance adaptations.

Another more complete example involves *Notothenia coriiceps* from Marion Island (Gon *et al.*, 1995). Although this population lives north of the Antarctic Polar Front, it possesses antifreezes and aglomerular kidneys. Its presence at Marion Island is probably the result of dispersal from the area of the Scotia Sea by the Antarctic Circumpo-

lar Current during the last 0.25 to 0.50 million years - insufficient evolutionary time for these freezing resistance adaptations to have been lost. Antarctic stocks (sometimes called *N. neglecta*) and sub-Antarctic stocks of *Notothenia coriiceps* probably represent a single wide ranging species since both stocks possess freezing resistance adaptations.

We should note that the position of the Antarctic Polar Front has shifted over geologic time. During the late Miocene (6.5-5.0 Ma), cold water and the position of the Front were north of the current location (Kennett, 1982). Marion Island and its fish fauna, however, are too young to have been influenced by this event - the oldest volcanic rocks on Marion Island are dated at 0.276 Ma (Walton, 1985).

Use divergence times inferred from molecular data to contribute to the discussion about the timing of palaeoenvironmental events and their possible role as vicariant events influencing the diversification of notothenioids

It is to our benefit to continue monitoring advances in Antarctic paleontology and geology. We gain information on composition of fossil fish faunas as well as dates for historical events that may have influenced the evolution of notothenioids. We could take an active role by contributing information on divergence times estimated from molecular data. Do these correspond to hypothesized vicariant events?

Although the existence of a regularly ticking molecular clock is controversial, I think that this information is extremely useful for our purposes. Do molecular divergence times for notothenioids correspond with the geologic (isotopic) dating of vicariant events such as the establishment of the Antarctic Circumpolar Current and with periods of decay of the ice sheet (the Webb-Harwood hypothesis considered below), when additional shelf habitat might have been available to fishes? Since the fossil record for notothenioids is limited, data providing a time frame for the appearance of any component of the group are worthwhile for examining hypotheses about the origin and diversification of notothenioids. Divergence times also hold promise for determining whether or not cladogenesis in notothenioids was punctuated (bursts of rapid evolution separated by periods of quiescence).

Divergence times estimated from molecular data are beginning to appear (Bargelloni *et al.*, 1994, 1995; Ritchie *et al.*, 1996). The estimates of Bargelloni *et al.* (1994, 1995) suggest that bovichtids diverged 57-45 mya whereas the rest of the notothenioid stock diversified rapidly under cooling conditions about 15-10 mya. Cladogenesis within the Trematominae and Channichthyidae may have taken place as recently as 4.5-2.5 mya, possibly under conditions of glacial instability.

Webb, Harwood and colleagues have hypothesized that small ice sheets have advanced and retreated a number of times in the past 14 Ma. Their recent discovery of unfossilized *Nothofagus* (southern beech) stems and leaves, dating from about 3 mya, suggests that the Antarctic climate was considerably warmer more recently than had ever been suspected. There may have been a terrestrial ecosystem within a few hundred km of the South Pole. Furthermore, on one or more occasions during the Pliocene, ice sheet retreat and rising sea levels opened several types of additional habitat for fishes. As recently as 2.5 Ma large marine embayments reached deep into the continent and, although more limited in extent, interglacial fjords developed between mountain ranges (Webb, 1990; Webb and Harwood, 1991). Partial deglaciation caused isostatic rebound of the continent with shelf waters restored to depths of 100-200 m. Study of diatom assemblages indicates that productivity was also increasing at this time (Harwood, 1991).

These findings call into question the longstanding assumption, based on oxygen isotopic data, that mid Pliocene water temperatures were near or below 0°C. Perhaps our thinking about the evolution of notothenioids has been biased toward the influence of "cold" vicariant events (circum-Antarctic currents, falling temperatures, advancing ice, ice scour of the continental shelf) in promoting phyletic diversification. There is no doubt that these events were important in the initial diversification of some notothenioids. Is it possible, however, that Pliocene (4.8-2.5 Ma) episodes of relative warmth and partial deglaciation were important in the later diversification of notothenioids living near the Antarctic coast? Or as phrased more provocatively by Harwood (1991, p. 671): "Is the Antarctic interior environment (fjords, local basins, etc.) more conducive to vicariant evolutionary radiation than the well-mixed Southern Ocean"?

Divergence times for some notothenioid clades coincide with this hypothesized period of glacial instability. In response to the question raised by Harwood, we can say that generally greater physical and trophic complexity of the habitat would be expected to enhance diversification. Isolation of populations might be more easily accomplished in interior habitats not subject to major currents. While interior marine habitat may not be more conducive to speciation, it is certainly a possible site of evolutionary diversification that we have not previously considered. It is difficult to say how this influenced the evolution of notothenioids. It could be hypothesized that rising sea levels and increased nearshore benthic and pelagic habitat could have promoted diversification within the Trematominae. Divergence times based on molecular data suggest that much of the phyletic diversification within *Trematomus* took place within the last few million years. As mentioned previously, it is paradoxical that *Patagonotothen*, the most speciose notothenioid genus, is largely confined to the relatively warm and shallow waters of southern South America.

The Webb-Harwood hypothesis has not gone unchallenged. Burckle and Pokras (1991), for example, think that the *Nothofagus* material from the Beardmore Glacier is the remains of an Oligocene-early Miocene relict assemblage rather than a Pliocene refugium. They also contest the existence of relatively warm marine embayments and the deglaciation of East Antarctica. Based on isotopic data, Denton *et al.* (1991) maintain that Antarctic ice volume during the Pliocene was never less than today.

Focus our studies on both the microevolutionary and macroevolutionary level

We have previously considered a number of macroevolutionary problems (i.e., evolution above the level of the species). Microevolution is evolutionary change within a species resulting from the differential survival of individuals or populations in response to natural selection. It is important because genetic (intraspecific) diversity is the raw material upon which evolutionary process act. We could use a combination of molecular and morphological approaches to examine microevolutionary questions.

There are few studies of molecular diversity among populations of notothenioid species, and those that have been conducted are aimed at stock recognition for fishery purposes. For example, using restriction endonuclease enzymes, Williams *et al.* (1994) examined genetic heterogeneity in the mitochondrial DNA (mtDNA) among five populations of *Champsocephalus gunnari* from the Kerguelen shelf area. They found no significant heterogeneity among fishes from any of these localities, although previous studies has suggested the existence of distinct stocks based on morphological and meristic characters and on differences in the time of spawning. These populations may have been sepa-

rated too recently to exhibit genetic isolation or there may be low level interchange of individuals maintaining homogeneity in mtDNA. In any event, there is discordance between answers inferred from molecular and morphological data. This is not surprising considering the possibility that meristic characters have been influenced by local environmental conditions during larval development whereas mtDNA has not.

It would be desirable to know if sibling or cryptic species are common among notothenioids. Although sibling species are nearly identical in appearance, they are true species as evidenced by reproductive isolation. Usually a decoupling of morphological and ecological divergence leads to sibling species (Knowlton, 1993). Some sibling species, for example, possess significant genetic differences (value of Nei's genetic distance > 0.5).

We have a possible example of sibling species within *Trematomus bernacchii* from McMurdo Sound. This was first alluded to by McDonald *et al.* (1987) in their paper on protein polymorphism of seven McMurdo nototheniids. The cryptic population of *T. bernacchii* has a large white patch in the occipital region. McDonald *et al.* suggest it might be distinct from *T. bernacchii*, but Nei's distance is only 0.105. It would be desirable to have information from other families of molecules. Given the state of our knowledge in the molecular systematics of notothenioids, it may be presumptuous to base taxonomic decisions on data from a single class of molecules.

Incorporate marine biodiversity issues as a component of our research

Whether recognized or not, we are already doing this. In our evolutionary studies of Antarctic fishes we are really seeking to answer a series of questions relating to the origin and nature of Antarctic biodiversity. Why is the modern fauna unlike the preceding fossil faunas as well as the shelf faunas of other southern continents? Why do modern notothenioids contribute so heavily to Antarctic fish biodiversity at both the organismal and ecological levels?

We can consider biodiversity at three levels: genetic (intraspecific), organismal (species) and ecological (communities) (Harper and Hawksworth, 1994). Since genetic biodiversity was considered above, I will mention only organismal and ecological diversity here. On a global scale, notothenioids are not very diverse if we simply count species or higher level taxa. As we have seen, however, they contribute heavily to organismal (species) diversity in the Southern Ocean and especially in the coldest shelf waters.

Therefore notothenioid diversity is multiplied if we consider ecological diversity - they are not just a suborder of middle sized benthic fishes. The single family Nototheniidae includes species that as adults are cryopelagic, pelagic, semipelagic, epibenthic as well as benthic. They range in size from 50 g to 90 kg. Their ecological diversity is further enhanced by the ontogenetic habitat shifts that are experienced by larvae and juveniles of many species - species with complex life cycles contribute extra biodiversity to a region (Harper and Hawksworth, 1994). We do notothenioids a great injustice if we consider only their species diversity. Their ecological diversity is noteworthy both within the order Perciformes (9,293 species) and the division Teleostei (23,637 species).

CONCLUSION

This paper has given me the opportunity to raise questions and to identify a few objectives dealing with the evolution of Antarctic fishes. Like many large scale organismal phenomena, some of these evolutionary questions will have no clear answers. Over the next few years, the component groups of the Fishes of the Antarctic Ocean Network will be doing the difficult part, which is also the most interesting - performing the research and providing testable hypotheses.

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